

SOME WOOD ANATOMICAL, PHYSIOLOGICAL, AND SILVICULTURAL ASPECTS OF SILVER FIR DIEBACK IN SLOVENIA (NW YUGOSLAVIA)

by

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Summary

Silver fir dieback in Slovenia (NW Yugoslavia) was evaluated, and growth suppression and some physiological and anatomical aspects of growth ring formation were studied. The drastic growth suppression after 1950 was reflected in poor basal area increment, and by discontinuous as well as missing rings. Only in the most diseased trees the height increment was affected. Generally latewood percentage and tracheid dimensions remained unchanged. The physiological mechanism of wetwood formation in sapwood of fir is discussed and compared with red heart formation in beech. On the basis of preliminary experiments, osmotic transport is suggested from sapwood to heartwood through the intermediate dry zone.

Dieback is significantly correlated with microsite factors such as rockiness and stoniness ($r = 0.47^*$), soil cover continuity ($r = 0.55^{**}$), and proximity of forest roads ($r = 0.43^*$).

Key words: *Abies alba* Mill., increment, tracheid length, vitality, wetwood formation, site factors.

Introduction

According to surveys conducted by the Institute for Forest and Wood Economy in 1985, the condition of silver fir (*Abies alba* Mill.) in Slovenia is as follows: 6.1% apparently undamaged; 9.5% slightly damaged; 14.4% damaged; 23.3% seriously damaged; 46.7% dying. A study of wood structure, changes in increment, and of wetwood formation was therefore undertaken in order to gain a better understanding of the background of this alarming decline of silver fir in NW Yugoslavia.

Materials and Methods

Twenty-two trees of silver fir were selected from a representative silver fir/beech forest association (*Abieti-Fagetum dinaricum omphalodetosum & hacquetietosum*) in the Slovenian Karst in March 1985. A detailed analysis of forest vegetation was made according to the Zürich-Montpellier method around each of the trees, and microsite parameters such as relief, exposure, slope, surface, bedrock thickness,

continuity of ground cover, stoniness and rockiness, and distance to forest roads were recorded. A floristic similarity quotient was computed for comparison of the different vegetation inventories, and correlations were determined between microsite factors and fir dieback.

Trees were rated on visual aspects as follows: 1) apparently unaffected (trees 24, 25, 26, 27, 29); 3) with severe leaf area reduction, frequently accompanied by epicormic branches (trees 3, 4, 6, 7, 8, 22, 23); and 2) with characteristics intermediate between 1 and 3 (trees 9, 10, 11, 15, 16, 17, 18, 19, 21, 28). From each tree eleven disks were taken. All trees were dominant or codominant, 142–236 years old, with a breast height diameter of 43 to 74 cm and a total height ranging from 24 to 36 m. For all trees stem and tree ring analysis was carried out, and growth in height, volume, diameter and basal area were determined. At three levels (breast height, crown base and crown centre) the radial distribution of moisture content was determined gravimetrically.

For two trees rated 1 (26 and 27) and two rated 3 (7 and 23) the latewood percentage was determined (cf. Mork, 1928) and statistically evaluated at three height levels for the periods before and after 1950, the presumed date for the onset of fir dieback. Tracheid length and tracheid wall thickness were determined for two apparently healthy and two diseased trees in the wood formed after 1950.

For testing the possibility of osmotic water transport from sapwood to wetwood through the dry zone, the latter acting as a 'semi-permeable membrane', a simple experiment was designed. Disks from the dry zone of 2–4 mm thickness and 38 mm in diameter were isolated and positioned between expressates of wetwood and sapwood, and water flow was assessed.

In addition, long term visual observations were systematically carried out on 2383 trees from seven areas throughout Slovenia between 1964 and 1982 according to the IUFRO silvicultural classification with added estimates of dieback symptoms.

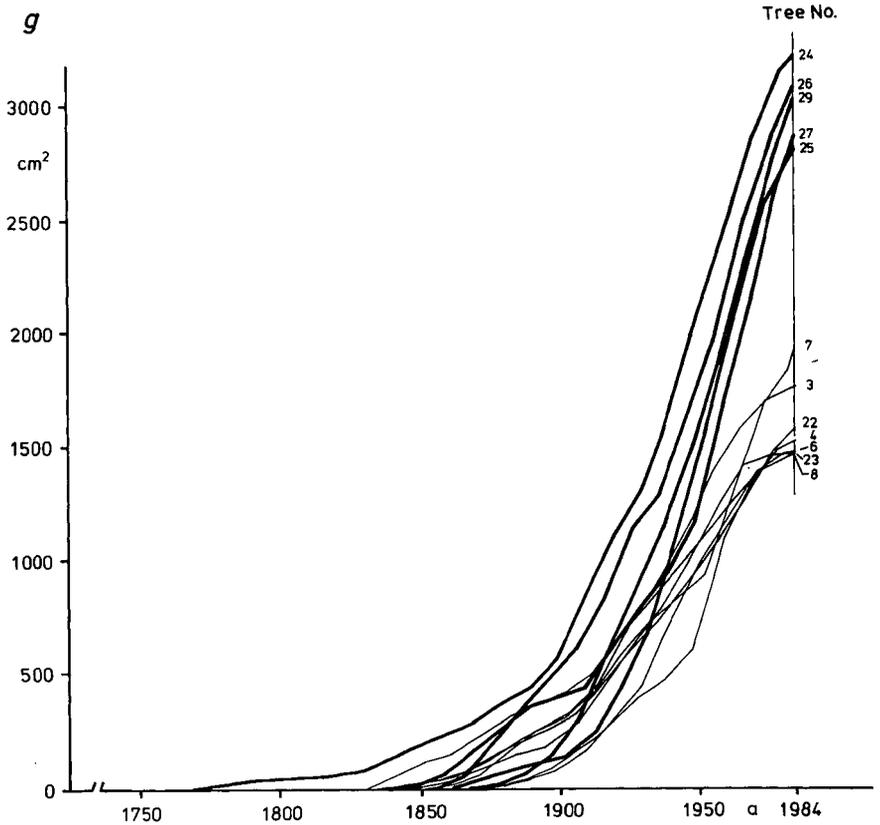


Fig. 1. Comparative analysis of basal area growth (g) at breast height of five apparently unaffected (bold lines) and seven severely diseased trees (thin lines).

Results and Discussion

Depending on the intensity of the damage, diseased trees always exhibit a more or less pronounced decrease in basal area growth from the early fifties onwards (Fig. 1). In eight test trees (3, 4, 6, 7, 8, 10, 21, and 23) an additional suppression was observed after 1970. Unlike observations in Germany (Bauch, 1983), the dry summer of 1976 did not affect tree growth to any great extent.

Annual ring width diminished drastically in the basipetal direction in diseased trees (Fig. 2), presumably because of pronounced physiological gradients. In the most severely affected trees discontinuous and missing rings were recorded at increasingly higher stem levels (Fig. 3). This can be attributed to the rapidly decreasing leaf area. There is evidence that the cambial activity is largely regulated by basipetal flow of compounds synthesised in the crown, especially

carbohydrates and hormones. Any external influence on the terminal growth (e.g., air pollution, water stress, etc.) of the leaf primordia and on the subsequent expansion of these primordia may be expected to play some contributory role in growth control (cf. Kozłowski, 1971). Moreover, life crown ratio, total leaf surface area, and metabolic activity will influence the annual increment along the bole. As trees age and the lower branches become physiologically inefficient or pruned, the relative height at which maximum ring width occurs gradually moves upward. In diseased trees with drastically reduced leaf area from sites affected by air pollution a similar but even more pronounced upward shift of maximum ring width is observed.

For growth suppression in relation to social position of trees, the same holds true. Here we also find a gradual reduction of xylem produc-

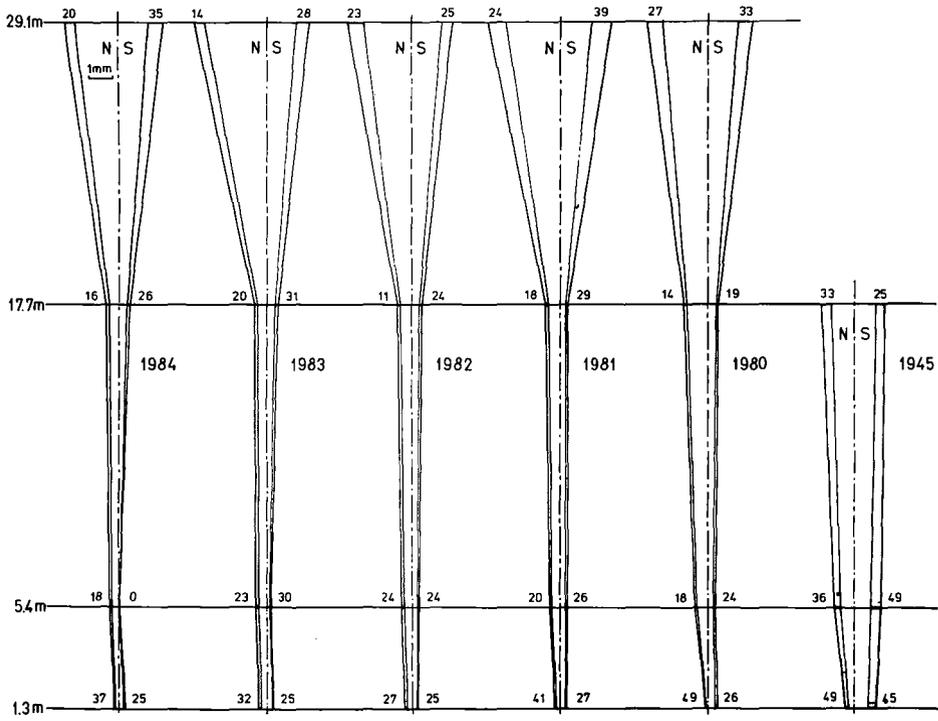


Fig. 2. Severely diseased tree no. 7: vertical distribution of annual ring width and latewood percentage (shaded; small figures) for the last five years of growth and for 1945, when the tree was presumably healthy.

tion and a higher proportion of total xylem being deposited at upper stem levels. With progressing suppression the cambium near the stem basis produces only discontinuous rings or none at all, so that the growth is more and more restricted to the upper parts only (Kozłowski, 1971). In addition cambial activity is often confined to shorter periods in suppressed trees when compared with dominant trees. Kozłowski and Peterson (1962) observed a progressive delay in the onset of cambial activity in the lower part of the stem with increasing suppression in *Pinus resinosa*. Severe internal water stress may have similar effects, resulting in discontinuous and missing rings. It seems that our preliminary observations on diseased trees affected by pollution show similar changes.

Height growth was only affected in the most severely affected trees (Fig. 4). Apparently the terminal shoot suffers last, so that height growth is hardly if at all affected by tree vitality as judged from crown appearance.

Latewood percentage showed no significant differences between diseased and apparently healthy trees. Our results were similar to those of Ylinen (1951) who found maximum values in rings of 1–2 mm and lower latewood percentages for both wider and narrower rings in Scots pine (Fig. 2). The transition between earlywood and latewood was typically more abrupt in the outer rings of diseased trees. We did not find an increase in latewood percentage as had been reported by Eckstein and Liese (1974) and Eckstein et al. (1981).

According to Larson (1973) radial tracheid diameter is regulated by a growth hormone produced by the needles while they are actively elongating, whereas wall thickness is closely correlated with increased availability of assimilates. Although both factors originate in the needles, they are physiologically independent and their maximal effectiveness occurs at different times. Since both processes involve transport, physiological gradients are formed

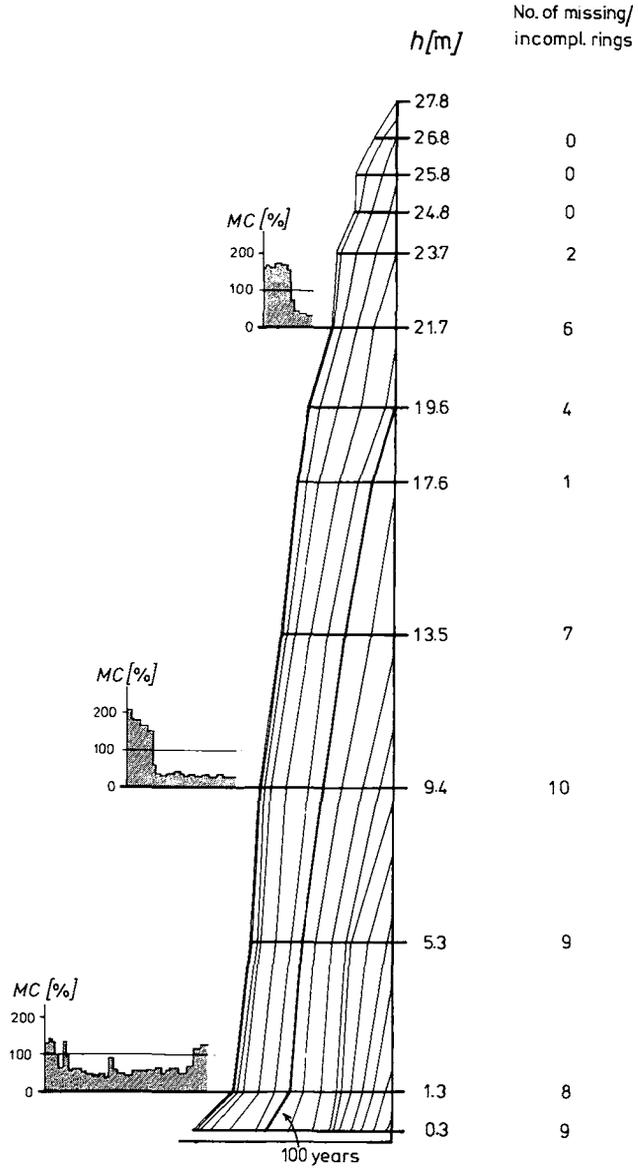


Fig. 3. Severely diseased tree no. 23 (age 158 years, total height 27.8 m, diameter at breast height 46 cm): stem analysis, distribution of moisture content (MC) and number of missing and discontinuous rings at various levels after 1975.

along the stem, and the tracheid produced will vary both with position in the stem and time of formation in the growth ring. As a tree increases in size and age, physiological stem gradients are

drastically altered. The initiation of latewood is attributed to a decreasing supply of auxin following the cessation of terminal growth. An abrupt early-latewood transition is often asso-

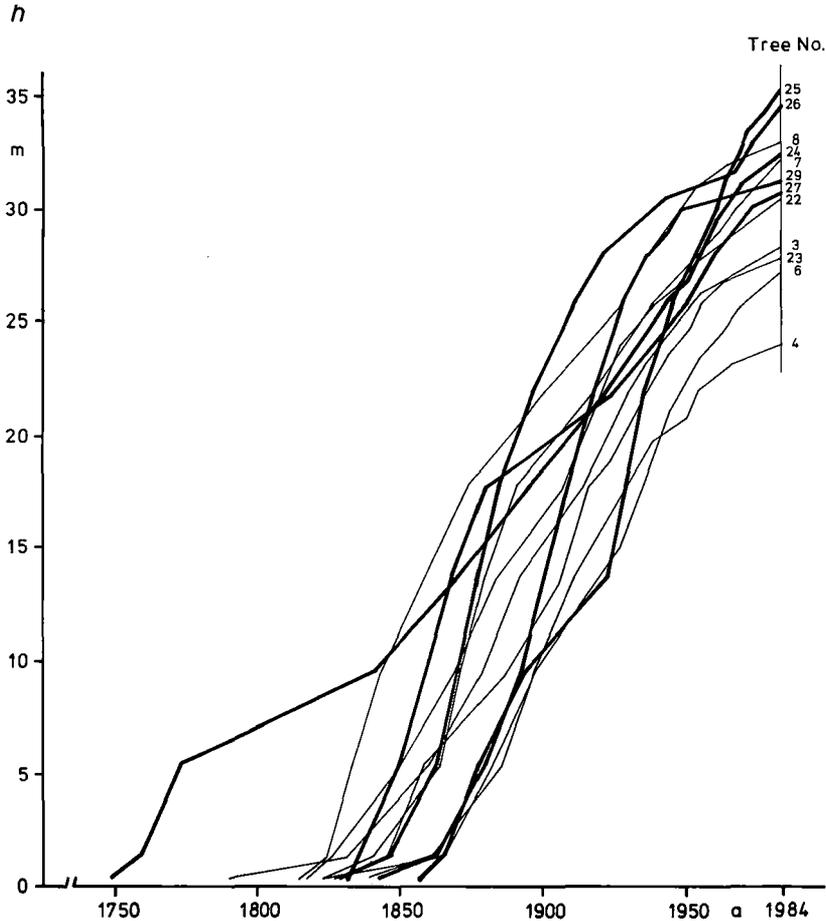


Fig. 4. Comparative analysis of height growth (h) of five apparently unaffected (bold lines) and seven severely diseased trees (thin lines).

ciated with growth reduction because the cessation of needle elongation and photosynthetic maturity tend to coincide when crown vigour declines. On the other hand, when physiological gradients overlap or interact, transitional wood is produced which is common in young trees and wide rings of older trees. It is possible to explain the observed abrupt early-latewood transition in the basal parts of diseased trees using a similar scenario as the one proposed by Larson (1973) summarised above.

Our preliminary measurements of tracheid length and cell wall thickness in diseased and apparently healthy trees did not reveal significant differences, thus not confirming the find-

ings by Bauch et al. (1979) or Eckstein et al. (1981), who found a decrease and increase, respectively.

In conclusion, it can be repeated that with respect to growth characteristics and wood structure, the diseased trees seem to behave similar to suppressed trees suffering starvation of the cambium or to trees suffering internal water stress.

All trees studied revealed more or less pronounced wetwood formation (cf. Bauch, 1973). Certain forms of wetwood are considered as symptoms of fir dieback (Bauch et al., 1979). In *Abies alba* two types of wetwood are generally recognised: wetwood developing in the

previously formed light heartwood, and irregular or linguiform wetwood extending into the sapwood.

There is no general agreement on the causes of wetwood in living trees (Hillis, 1977). According to Ward and Zeikus (1980) invasion and survival of bacteria appears to be an essential prerequisite for the initiation and formation of wetwood. Because not all isolations from wetwood yielded bacteria, the bacterial origin of wetwood is not universally accepted and a purely physiological, autonomous origin is quite possible. It should be kept in mind that bacteria, when present, may not be the direct cause of wetwood formation. They may become established after the wetwood conditions occur. Furthermore, bacteria have also been isolated from trees with apparently normal wood and from the sapwood and heartwood of wetwood trees (Ward & Zeikus, 1980). Fungi occur in the wood only at a later stage when the crown of the tree has dried up completely (Bauch et al., 1979).

The formation of irregular wetwood in the sapwood of *Abies alba* is preceded by visible dehydration; a situation which resembles the formation of red heart in beech (cf. Torelli, 1984). It is hypothesised here that in dying fir trees with accelerated defoliation the sapwood is not transformed into heartwood but intensively dehydrated. This may then be followed by the formation of wetwood. The dry zone intermediate between wetwood and sapwood would then be the final result of sapwood dehydration caused by drastic crown reduction in combination with other abiotic or biotic factors.

In this context it is interesting to note that Coutts (1976) observed dry zones forming in the sapwood of conifers in response to infection by *Fomes annosus*. The water was withdrawn from infected parts of logs into uninfected parts, probably by the release of hydrostatic tension. Coutts postulated that *Fomes annosus* infection broke the sealing mechanism by destroying pit tori or cell walls. In stems of *Abies grandis* inoculated with *Fomes annosus* he observed dehydration which occurred far beyond the limit of fungal infection, especially in the 'susceptible' inner sapwood. He concluded that some substance diffusing from the infected region might be responsible for initiating replacement of water in tracheids by gas, through its action on living parenchyma cells. Dry zones also formed after a few days in living conifer xylem injected with dilute solutions of toxic chemicals (Coutts, 1977). The results were interpreted as showing that substances produced by or liberated from dying parenchyma cells might cause gas embolism in water columns

under tension. In a further experiment Coutts and Risbeth (1977) were able to induce dehydration and subsequent wetwood formation by injection of mercury chloride in the sapwood of standing trees of *Abies grandis*.

In our opinion the dehydration in the dry zone might have the same effect on the ray parenchyma cells as the dilute solutions of toxic chemicals, viz. gradual cell death with altered metabolism (cf. Nobuchi et al., 1984), including ethylene production (cf. Shigo & Hillis, 1973; Hillis, 1977). However, more experimental data are obviously needed to test this hypothesis.

Because sapwood, wetwood and the dry zone between them coexist in the living tree, we hypothesised the occurrence of osmotic water transport from sapwood to wetwood. Our preliminary experiments with the expressates from wetwood and sapwood separated by a dry zone containing a thin sheet of wetwood with a hypothetical 'seal' between them at least leaves this possibility open. Permeability of the 'membranes' appeared to be very poor, however, enabling only a waterflow of 1.5 cm³ in 12 hours or none at all in some of the trials. When the 'osmotic' transport occurred, the dry zone remained dry. In other cases they became soaked. The experiments are being continued. Coutts and Risbeth (1977) suggested that the movement of water into wetwood might be based on an established difference in osmotic pressure between wetwood and sapwood brought about by the accumulation of metabolites in the former. Movement must take place across the intervening dry zone, a layer of tracheids blocked by gas bubbles but bridged by some living parenchyma cells (cf. Zimmermann, 1983). Furthermore Coutts and Risbeth stated that the physiological activity of the tree is involved. Formation of wetwood was prevented by a phloem block and did also not occur in detached stem segments. They observed that wetwood formed fastest in vigorous trees and at seasons of the year when metabolism was likely to be most active.

As noted before, the red heart in beech is surrounded by a similar dry zone which either itself, or more probably its innermost part only, might act as a 'semipermeable membrane', thus explaining the frequently observed increase of moisture content in the red heart (Torelli, unpublished; Fig. 5).

This hypothesis of a purely physiological mechanism of wetwood formation does not exclude the possibility of a localised pathological origin as described by Coutts (1976). An artificial phloem block (Coutts & Risbeth, 1977) may have the same effect as a dwindling supply of photosynthetic products and growth sub-

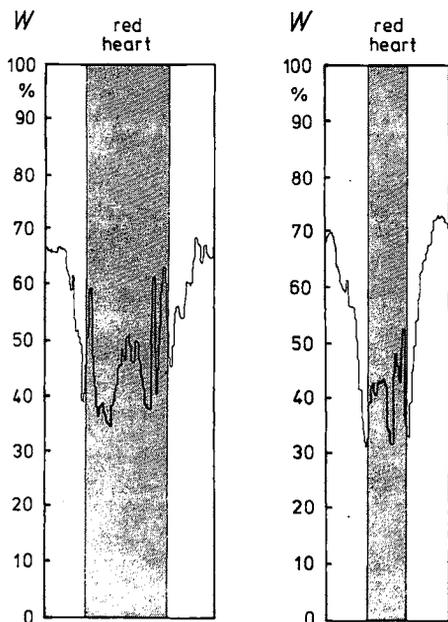


Fig. 5. Free water (W) distribution at one fifth of the total tree height in two beeches with red heart. Note the sharp decrease outside the red heart boundary and the coincidence of wetwood and red heart.

stances in dying trees: absence of wetwood formation. In our material, typical wetwood formation was absent or only poorly developed and localised in trees in the last stage of decline and with discontinuous and missing rings.

According to our field observations vitality varies in accordance with differences in microsite factors. Fir has been favoured in forestry practices in Slovenia, and has thus settled the whole microsite spectrum. This has caused a strong differentiation of fir vitality. Being limited in its capacity to adapt ecologically, silver fir reacts faster to harmful than to beneficial influences. A great number of trees rated as unvital at the beginning of the observation period in 1964 nowadays exhibit rapid decline.

Analysis of floristic similarity coefficients of the forest vegetation indicated a fairly large overall floristic similarity and little variability. From this one might conclude that growing conditions and stands from which the trees were taken, were quite uniform. Fir dieback appears independent of the site groups that can be recognised on floristic criteria. On the other

hand strong dependencies of dieback were found on the following microsite factors: rockiness and stoniness ($r = 0.47^*$); soil cover continuity ($r = 0.55^{**}$); and proximity of forest roads ($r = 0.43^*$). The already known mutual correlation between fir dieback and secondary crown formation ($r = 0.77^{**}$) and crown form ($r = 0.86^{**}$) could be confirmed again in our study.

The long term observations on 2383 sample trees from 1964 to 1982 (Robič, unpublished) show a close correlation between vitality and dieback (r ranges from -0.70^{**} to -0.76^{**}). The majority of trees which were recorded as highly vigorous at the beginning of the observation period remained so throughout, while trees in their immediate vicinity were declining or dying.

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